



Local population density and the activation of movement in migratory band-forming Mormon crickets

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The Mormon cricket, *Anabrus simplex* (Orthoptera: Tettigoniidae), is a flightless katydid that undergoes major outbreaks in western North America. Under outbreak conditions, Mormon crickets often form large cohesive migratory bands that can contain millions of individuals moving in unison across the landscape. Density-dependent phase polyphenism has been hypothesized as a behavioural mechanism underlying Mormon cricket band formation and movement based largely on the similarity between bands of Mormon crickets and those of migratory locusts. I tested this hypothesis by quantifying the effects of long-term differences in rearing density versus the short-term presence or absence of conspecifics on Mormon cricket movement behaviour across three different developmental stages. Rearing density and the presence of conspecifics both influenced Mormon cricket movement, but in distinctly different ways. Increases in the expression of walking-related behaviours were mainly induced by the short-term presence of conspecifics. The longer-term effects of high rearing density primarily influenced only turning-related behaviours. Developmental variation in activity levels was observed and indicates that developmental stage should be an important consideration in future analyses of Mormon cricket movement. Overall, these results suggest that interindividual interactions play a greater role in inducing the movement of migratory band-forming Mormon crickets than do endogenous behavioural-phase changes mediated by high local rearing density.

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The Mormon cricket is a flightless shield-backed katydid widely distributed throughout western North America. Outbreaks of this species can result in the formation of spectacular migratory bands that can be over 10 km long, several kilometres wide, contain dozens of insects per square metre, and travel up to 2.0 km per day (Cowan 1929; Wakeland 1959; MacVean 1987). These bands can cause major damage when they enter crop systems and usually require swift chemical control. In addition, they can also pose a public safety threat when large numbers of insects cross roadways, are crushed by passing vehicles, and thereby produce dangerously slick driving conditions (Gwynne 2001). Despite the economic and cultural significance of Mormon crickets in the western U.S., their biology, ecology and behaviour have been the focus of relatively few empirical studies (Cowan 1929; Wakeland 1959; MacVean 1987; Gwynne 2001).

Although untested, density-dependent phase polyphenism has been hypothesized as a behavioural mechanism

underlying Mormon cricket band formation and movement based largely on the similarity between migratory bands of Mormon crickets and those of migratory locusts (MacVean 1987; Cowan 1990; Pfadt 1994; Gwynne 2001). Phase polyphenism is a type of phenotypic plasticity that can involve a suite of behavioural, morphological and physiological changes that occur in response to changes in local population density (reviewed in Pener 1991; Pener & Yerushalmi 1998; Applebaum & Heifetz 1999; Simpson et al. 1999). High rearing densities induce phase changes that produce individuals with migratory phenotypes that often travel en masse, similar to the phenomenon observed in band-forming Mormon crickets. In locusts, the simultaneous expression of increased activity and increased attraction among individuals that have been reared at high population density (Simpson et al. 1999) is thought to account for the formation and movement of cohesive migratory hopper bands and adult swarms (Uvarov 1977).

A small number of katydids including Mormon crickets are thought to express phase polyphenism and some may even form huge flying swarms reminiscent of locusts (reviewed in Gwynne 2001). MacVean (1987, page 119) noted that the formation of migratory bands in the

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Mormon cricket 'bears a striking resemblance to phase transition in the African plague locusts', and Cowan (1990) stated that the Mormon cricket has gregarious and solitary phases similar to locusts. As with locusts, Mormon crickets often differ in colour between band-forming, outbreak and non-band-forming, nonoutbreak populations (MacVean 1987; Cowan 1990; Lorch & Gwynne 2000; Gwynne 2001). The locust and Mormon cricket literature also share terminology, with non-band-forming Mormon crickets commonly referred to as inactive solitary individuals (i.e. solitary phase) whereas those in band-forming populations are referred to as gregarious (e.g. Wakeland 1959; MacVean 1987, 1990; Lorch & Gwynne 2000; Gwynne 2001).

Although phase polyphenism has independently evolved a number of times in different insect lineages (Applebaum & Heifetz 1999), it is not the only underlying behavioural mechanism that can be hypothesized to account for the existence of migratory bands and the observed similarities between Mormon crickets and locusts under outbreak conditions. Indeed, a number of organisms do not express phase polyphenism, yet they form groups and show collective movement behaviour. In many cases, such as bird flocks, fish schools, and even the collective movement of bacteria (Ben-Jacob 2003; Couzin & Krause 2003), complex group-level behaviours can result from self-organization in which group-level patterns arise from relatively simple interindividual interactions (Camazine et al. 2001).

Although anecdotal accounts and strong opinions abound, there have been no published studies to date examining the behavioural mechanisms underlying Mormon cricket band formation and movement. To this end, I tested the hypothesis that band-forming Mormon crickets express density-dependent behavioural phase polyphenism. My data failed to support this hypothesis, but rather suggest that the short-term effects of stimuli provided by conspecifics play a much greater role in the activation of movement in band-forming Mormon crickets than do the longer-term effects of high rearing density.

METHODS

Experimental Design

I conducted a laboratory experiment to examine the behavioural effects of stimuli provided by conspecifics on the movement behaviour of migratory band-forming Mormon crickets. Using a two-way factorial design, I tested the long-term effects of high population density on behaviour by rearing individuals under either isolated or crowded conditions. The short-term behavioural effects of high population density as well as potential interactive effects were tested by assaying the behaviour of the isolated and crowd-reared insects either in the immediate presence or absence of conspecifics in the observation arena during the observation period. The experiment was conducted across three different developmental stages to test for developmental variation in behaviour. See Fig. 1 for a diagram detailing the experimental design.

		Rearing	
		Isolated (1 insect/cage)	Crowded (70 insects/cage)
Conspecifics	Absent (1 insect/arena)	Sixth instar (N = 35)	Sixth instar (N = 38)
		Prereproductive (N = 34)	Prereproductive (N = 34)
		Reproductive (N = 36)	Reproductive (N = 36)
	Present (5 insects/arena)	Sixth instar (N = 35)	Sixth instar (N = 36)
		Prereproductive (N = 31)	Prereproductive (N = 31)

Figure 1. Diagram of the factorial experimental design depicting all treatment combinations tested and their sample sizes. Insects were reared under isolated or crowded conditions (rearing treatment) and assayed in the arena either in the presence or absence of conspecifics (conspecifics treatment). Insects were assayed as sixth instars, prereproductive adults and reproductive adults to test for developmental variation in behaviour. Reproductive adults were not assayed in the presence of conspecifics.

Insects and Rearing Conditions

Insects for this experiment were collected on 26 March 2003 as recently hatched first instars emerging over a large area from eggs previously deposited by a Mormon cricket band in the vicinity of Oak City, Utah (39°21'6"N, 112°21'48"W). Insects to be reared under isolated conditions were individually collected into 50-ml plastic centrifuge tubes. Insects to be reared under crowded conditions were collected into two screen cages (34L × 34W × 48H cm, 125 insects/cage). Insects were fed Romaine lettuce and transported by vehicle to the USDA-ARS Northern Plains Agricultural Research Laboratory for rearing and observations.

Isolated and crowded insects were reared at 30°C, on a 14:10 h light:dark cycle in different buildings to prevent potential olfactory contact between rearing treatments. All insects were daily fed fresh Romaine lettuce and a 1:1:1 mixture of wheat bran, tropical fish food and birdseed. Isolated insects were reared individually in cylindrical clear plastic cages (15 cm height × 11.5 cm basal and 8.5 cm top diameter). Cages had wire mesh tops, a 2.5 × 13-cm strip of wire mesh glued vertically to the side of the cage to provide a roost, and were wrapped with white paper to visually isolate them from other cages. Cages were kept on trays lined with brown paper, which was replaced daily to minimize self-exposure to faeces and associated volatiles. The room housing the isolated cages underwent 12 complete air exchanges per hour, reducing the potential for olfactory exchange among the isolated

insects. In addition, air in both the isolated and crowded rearing rooms was continuously circulated through HEPA air purification systems (model 200 001, Bemis Manufacturing Company, Sheboygan Falls, Wisconsin, U.S.A.). Crowd-reared insects were maintained in a screen cage (34L \times 34W \times 48H cm) kept at a constant density of 70 insects/cage. Density was held constant by adding insects from a similarly maintained stock cage initially established with 100 insects.

Behavioural Assays

Behavioural observations were conducted at 30°C in a square (60 \times 60 \times 60 cm) white acrylic arena with Fluon-coated walls (Northern Products, Woonsocket, Rhode Island, U.S.A.) to prevent climbing. The floor of the arena was lined with brown paper that was replaced between each observation. The arena was illuminated with four 15-W fluorescent bulbs. Two were 45.75 cm long and the other two were 61 cm long, with lights of the same size mounted opposite each other 113 cm above the arena floor. Prior to being observed, all experimental insects were colour-marked by painting the dorsal surface of the pronotum white with Liquid Paper (Gillette Company, Boston, Massachusetts, U.S.A.). An individual insect was gently introduced into a blackened 266-ml plastic Solo cup (Solo Cup Company, Highland Park, Illinois, U.S.A.) internally coated with Fluon. The cup was inverted on a piece of white cardstock and the insect was allowed to settle for 5 min. The cardstock and cup were then placed in the centre of the observation arena, the cardstock gently slid from under the cup, and the insect was allowed to settle for an additional 1 min. To begin the observation, the blackened cup was slowly lifted out of the arena and the insect's movements were then continuously observed for 5 min. Observations were recorded on VHS tape with a colour CCD video camera centred 100 cm directly above the arena floor.

I randomly assigned isolated and crowd-reared insects (rearing treatment) to one of two short-term stimuli treatments, namely, to be assayed either in the presence or absence of conspecifics in the observation arena (conspecifics treatment) (Fig. 1). Insects assigned to the absence of conspecifics treatment were observed alone in the arena. Those assigned to the presence of conspecifics treatment were observed in the presence of four unmarked stimulus insects, two females and two males of similar age, taken from the crowd-reared stock cage. Position of the stimulus insects was standardized between observations by positioning them under blackened cups midway between the focal insect and the four corners of the arena. These stimulus insects were placed in the arena at the same time as the focal insects and similarly allowed to settle for 1 min prior to the observation period. Observations of insects in the presence of conspecifics were started by first lifting the cups of the stimulus insects followed by that of the focal insect. Observations of insects in the absence of conspecifics were initiated by lifting the cup of the focal insect. All insects were then observed continuously for 5 min.

I assayed behaviour of isolated and crowd-reared insects across three different developmental stages, sixth-instar nymphs (1–3 days postmoult), prereproductive adults (1–3 days postmoult), and reproductive adults (2 weeks postmoult) to test for the effects of developmental variation on movement behaviour and the response to population density (Fig. 1). Due to mortality within both rearing treatments and the difficulty of identifying individuals between moults among the crowd-reared insects, groups consisting of different individuals were assayed at each developmental stage. Reproductive adults were not assayed in the presence of conspecifics due to the potential for confounding effects of sex-related interactions on movement behaviour.

I quantified insect movement behaviours from video recordings using the EthoVision 4.0 ColorPro Video Behavioral Analysis System (Noldus Information Technology 2002) running on a Pentium 4, 2.8 GHz PC with an installed Pico video frame grabber. Location, displacement, and other movement parameters were determined automatically by the software using the grey scaling method to detect the insect. Video was digitized at a resolution of 640 \times 480 pixels and insects were tracked at a sample rate of six samples/s. Insect position was determined by the centre of the insect's marked pronotum. A threshold movement of 0.5 cm was used to differentiate true locomotion from position changes due to stationary shifts in body position or system noise.

I calculated six behavioural parameters, three related to walking and three related to turning, from the individual tracks to compare movement between treatments in general terms. These parameters were as follows: (1) walk time (%), percentage of the assay spent walking; (2) speed (cm/s), average distance moved per unit time; (3) distance (cm), total distance moved during the assay; (4) turn angle (°), average absolute change in direction between two consecutive samples; (5) turning rate (°/s), average absolute change in direction of movement per unit time; and (6) meander (°/cm), average absolute change in direction relative to distance moved. See Noldus Information Technology (2002) for detailed information about the calculation of these parameters.

Analysing tracks in discrete time steps as was done in this study does not adequately describe the entire turn made by an organism during the course of a move (Bell 1991; Turchin 1998). Despite this, however, such a technique is sufficient for comparisons of turn angles or turning rates made under different environmental conditions (Turchin 1998). Due to the way in which turn angle and turning rate were quantified in this study, it is important to point out that they would be expected to positively covary with the walking-related behaviour speed. This is because sampling changes in the heading of faster animals relative to slower ones while completing an identical turn will result in the recording of larger turn angles at a given sampling interval for the faster animals (Bell 1991). Importantly, the turning behaviour meander is calculated independently of an organism's speed and is of value in determining real differences in overall turning during the assay when significant effects of speed are present (Bell 1991).

Data Analysis

I analysed overall behavioural differences between treatment groups considering the entire suite of six behaviours simultaneously using a two-way factorial nonparametric multivariate analysis of variance (NPMANOVA) (Anderson 2001; McArdle & Anderson 2001). NPMANOVA uses a test statistic analogous to Fisher's F statistic calculated from a distance matrix generated from the original data. It can also be used for simple two-group multivariate comparisons analogous to a multivariate t test. P values are obtained using permutations. Behavioural data were transformed to z scores prior to analysis to standardize for differences in scale (Anderson 2001). Analysis was based on a Euclidian distance matrix among all behaviours under the permutation of residuals model for 9999 iterations.

NPMANOVA requires balanced sample sizes across factor levels. To satisfy this, I randomly subsampled the sixth instar, prereproductive adult and reproductive adult data sets to yield balanced sample sizes of $N = 35$, 31 and 36 individuals, respectively, at each rearing \times conspecifics factor level. To examine the effects of developmental stage and rearing density on the overall expression of movement, I randomly subsampled the data sets of all three stages to yield a balanced sample of $N = 31$ insects for each development \times rearing factor level. Since reproductive adults were not assayed in the presence of conspecifics, developmental variation in the response to conspecifics in the arena was not tested in this analysis. When significant overall treatment effects were found in the NPMANOVA, follow-up univariate Mann–Whitney U tests were conducted in StatView 5.0.1 (SAS Institute 1998) on complete data sets to examine the relative underlying contribution of specific behaviours. Sexual differences were not evident in any of the experiments as determined by comparisons with univariate Mann–Whitney U tests on all behaviours; thus, the sexes were grouped together for all the analyses presented here.

RESULTS

Among sixth-instar Mormon crickets, both rearing density and the presence or absence of conspecifics during the assay significantly affected the overall expression of movement behaviour. These effects are apparent in the significant main effects of rearing and conspecifics found in the NPMANOVA (Table 1). The interaction term was not significant. Follow-up examinations of the underlying univariate behavioural differences revealed that the significant main effects of rearing density and presence or absence of conspecifics were each due to changes in different suites of movement behaviour. Changes in rearing density primarily influenced the expression of turn-related behaviours, with turn angle and meander being expressed to greater degrees among crowd-reared insects. These differences in turning behaviour were expressed regardless of the presence or absence of conspecifics in the arena (Table 2, Fig. 2). On the other hand, the presence or absence of conspecifics during the assay affected the three walk-related behaviours, walk time, speed and distance,

with their expression being greater in the presence of conspecifics. These changes in walking behaviour were expressed regardless of the insects' rearing density (Table 2, Fig. 2).

Both rearing density and the presence or absence of conspecifics significantly affected the behaviour of prereproductive adult Mormon crickets as well (Table 1). The overall interaction term was not significant (Table 1). Rearing density had a modest effect on movement that was only apparent among insects assayed in the presence of conspecifics (Table 2, Fig. 2). Among these insects, two turning behaviours, turn angle and meander, were greater among crowd-reared insects, whereas one walking behaviour, speed, was greater among the isolation-reared insects (Table 2, Fig. 2). In contrast to these relatively slight effects of rearing density on the movement behaviour of prereproductive adults, the presence of conspecifics had a major effect and induced significant increases in all six walking and turning-related behaviours regardless of the insects' rearing density (Table 2, Fig. 2).

Among reproductive adults, rearing density also had a significant overall effect on movement behaviour (NPMANOVA: $t_{71} = 2.9509$, $P < 0.0001$). Values for two turning-related behaviours, meander and turn angle, were significantly greater among crowd-reared insects, whereas speed, a walking behaviour, was expressed to a greater degree among isolation-reared insects (Table 2, Fig. 2). Reproductive adults were not assayed in the presence of conspecifics.

The movement behaviour of the insects varied across developmental stages. Comparison of the movement of isolation- and crowd-reared insects as sixth instars, prereproductive and reproductive adults in NPMANOVA revealed significant main effects of both density and development (Table 3). The interaction term was not significant, indicating that although there was developmental variation in behaviour, the response to rearing density did not dramatically change over the course of development sampled here (Table 3). Pairwise comparisons between different developmental stages suggest that the significant effect due to developmental stage was mainly due to differences in movement behaviour between the prereproductive adults and the other developmental stages. Behaviour of the prereproductive adults was significantly different from that of the reproductives for insects reared under both isolated (NPMANOVA: $t_{61} = 1.9709$, $P = 0.023$) and crowded (NPMANOVA: $t_{61} = 2.1563$, $P = 0.0052$) rearing densities. From Fig. 2 it can be seen that these differences were due to relative inactivity among the prereproductive insects. All other comparisons between developmental stages were not significantly different.

DISCUSSION

My results failed to support the hypothesis that band-forming Mormon crickets express extensive density-dependent behavioural phase changes. Instead, these findings suggest that short-term interactions between individuals play a much greater role in the activation of

Table 1. Nonparametric MANOVA of the overall effects of rearing density (rearing) and the presence or absence of conspecifics (conspecifics) on the movement behaviour of sixth-instar and prereproductive Mormon crickets

Stage	Source	df	SS	MS	F	P
Sixth instar	Rearing	1	29.6412	29.6412	5.7625	0.0013
	Conspecifics (CS)	1	100.7865	100.7865	19.5938	0.0001
	R×CS	1	4.0154	4.0154	0.7806	0.4835
	Residual	136	699.5568	5.1438		
	Total	139	834.0000			
Prereproductive	Rearing	1	22.2959	22.2959	4.0623	0.0116
	Conspecifics	1	53.9939	53.9939	9.8376	0.0001
	R×CS	1	3.0903	3.0903	0.5630	0.6213
	Residual	120	658.6200	5.4885		
	Total	123	738.000			

an individual's movement than do longer-term behavioural changes induced by high rearing density.

The observed similarity in migratory band formation and movement between locusts and Mormon crickets

fueled speculation that Mormon crickets might express density-dependent behavioural phase polyphenism similar to that known to occur in locusts (MacVean 1987; Cowan 1990; Pfadt 1994). This does not appear to be the

Table 2. Mormon cricket behavioural changes induced by isolated (I) versus crowded (C) rearing conditions and the immediate presence (P) versus absence (A) of conspecifics

Stage and rearing	Conspecifics	Behaviour	<i>U</i>	<i>P</i>	Direction
Sixth-instar nymphs					
Isolated vs Crowded	Absent	Meander	440	0.0116	C>I*
		Turn angle	432	0.009	C>I
Isolated vs Crowded	Present	Meander	381	0.0042	C>I
		Turn angle	337	0.0008	C>I
Isolated	Absent vs Present	Distance	200	<0.0001	P>A
		Speed	351.5	0.0021	P>A
		Walk time	163.5	<0.0001	P>A
		Turning rate	334.5	0.001	P>A
Crowded	Absent vs Present	Distance	370	0.0007	P>A
		Speed	366	0.0006	P>A
		Walk time	335	0.0002	P>A
		Turning rate	485.5	0.0316	P>A*
Prereproductive adults					
Isolated vs Crowded	Absent	None	—	—	—
Isolated vs Crowded	Present	Speed	294	0.0086	I>C
		Meander	166.5	<0.0001	C>I
		Turn angle	171.5	<0.0001	C>I
Isolated	Absent vs Present	Distance	227	<0.0001	P>A
		Speed	272.5	0.0006	P>A
		Move time	207.5	<0.0001	P>A
		Meander	328	0.0075	P>A
		Turn angle	348	0.0162	P>A
		Turning rate	271	0.0006	P>A
Crowded	Absent vs Present	Distance	252.5	0.0003	P>A
		Speed	257	0.0004	P>A
		Move time	255	0.0003	P>A
		Meander	300.5	0.0027	P>A
		Turn angle	277.5	0.001	P>A
		Turning rate	217.5	<0.0001	P>A
Reproductive adults					
Isolated vs Crowded	Absent	Speed	464	0.0378	I>C*
		Meander	366	<0.0001	C>I
		Turn angle	367	<0.0001	C>I

Only significant univariate differences underlying the overall main treatment effects of rearing and conspecifics detected during multivariate analyses are shown. Asterisks (*) indicate differences that were not significant following a Dunn–Sidak method sequential Bonferroni correction for multiple comparisons (Sokal & Rohlf 1995). Box plots comparing all behaviours are presented in Fig. 2.

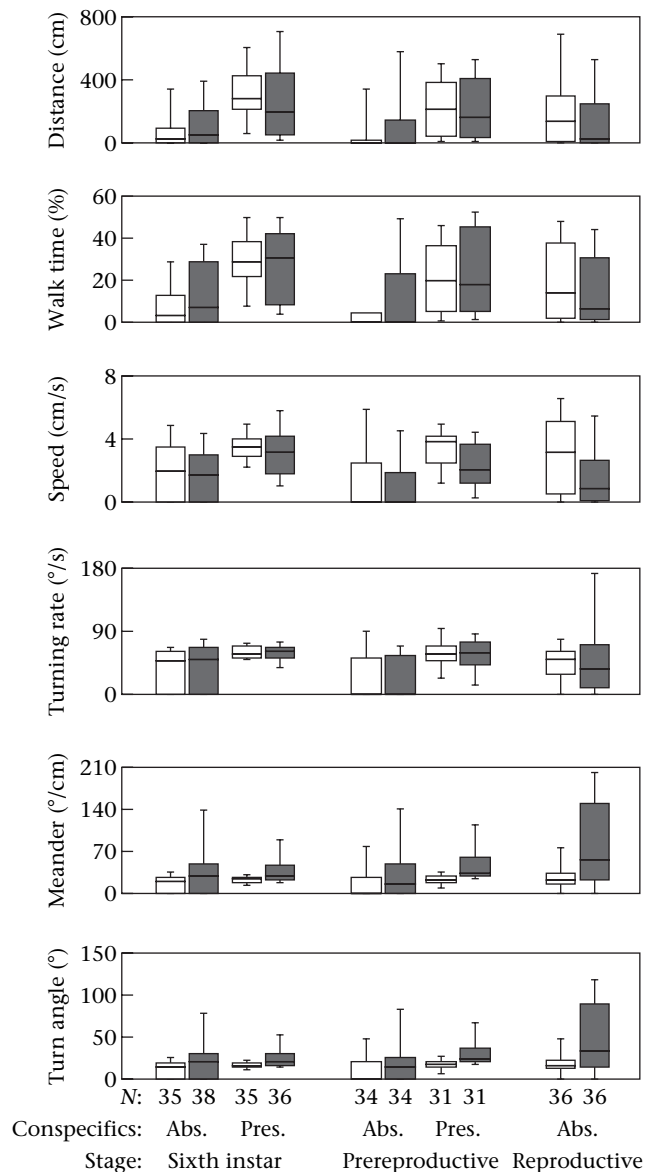


Figure 2. Movement behaviour of Mormon crickets from a band-forming population reared under either isolated (□) or crowded (■) conditions and assayed either in the presence or absence of conspecifics. Each box plot displays the median value with the ends of the boxes representing the 25th and 75th percentiles and the ends of the lines representing the 10th and 90th percentile values. See Tables 1 and 3 for overall multivariate analyses and Table 2 for univariate analyses. Abs.: absent; Pres.: present.

case. Among band-forming Mormon crickets, stimuli provided by the immediate presence of conspecifics played a much larger role than rearing density in the activation of movement behaviour (Table 2, Fig. 2). This situation is quite different from that observed in locusts, where individuals reared at high density are much more active than those reared in isolation and their density-dependent behavioural differences are expressed even in the absence of conspecifics (Roessingh et al. 1993). Differences in rearing density induced only minor behavioural changes in Mormon crickets, most notably in the expression of turn-related behaviours. In contrast, the presence of

Table 3. Nonparametric MANOVA of the overall effects of rearing density (rearing) and developmental stage (development) on Mormon cricket movement behaviour

Source	df	SS	MS	F	P
Rearing (R)	1	45.7859	45.7859	8.2045	0.0001
Development (D)	2	41.1527	41.1527	3.6871	0.0028
R×D	2	18.5579	9.2789	1.6627	0.1340
Residual	180	1004.5036	5.5806		
Total	185	1110.0000			

conspecifics resulted in much greater expression of both walking and turning-related behaviours (Table 2, Fig. 2).

The possibility that epigenetic effects influenced the behaviour of the insects used in this experiment cannot be ruled out at this time. The importance of epigenetics in ecology and evolution has become widely recognized (Mousseau & Fox 1998). Among locusts, for example, the density experienced by adults during mating and oviposition can have a dramatic effect on the behavioural phenotype of their offspring (Pener 1991; Islam et al. 1994a, b; Simpson et al. 1999). If present, similar epigenetic effects could have affected the outcome of this experiment by obscuring the behavioural effects of rearing density if the behaviour of the insects from the band-forming population was influenced by the density of their parents. Regardless, the impact of the presence of conspecifics on Mormon cricket movement independent of their rearing history implicates interindividual interactions as an important mechanism underlying the group-level behavioural patterns of bands observed in the field.

Interindividual interactions among Mormon crickets in the present study played a dramatic role in the activation of their walking-related behaviours. In fact, the only walking-related behaviour to differ significantly in comparisons of isolation- and crowd-reared insects was speed (Table 2). In both of these cases, however, speed was actually lower among the crowd-reared insects relative to those reared under isolated conditions. The biological relevance of this seemingly counterintuitive result is unknown. This slight difference in walking behaviour between isolation- and crowd-reared insects was in sharp contrast to the differences between insects assayed in either the absence or presence of conspecifics. All the walking-related behaviours, distance, speed and walk time, were expressed to a significantly greater degree among insects in the presence of conspecifics. In addition to these increases in walking-related behaviours, a number of turning-related behaviours were also positively influenced by the presence of conspecifics regardless of the insects' rearing density (Table 2, Fig. 2). This effect is most notably apparent in the response of the prereproductive insects in which all of the behaviours quantified in this study were expressed to a significantly greater degree in the presence of conspecifics (Table 2, Fig. 2). It is difficult to extrapolate the relationship between the walking and turning-related behaviours observed here to conditions within a band because the insects were confined to an artificial arena. However, the importance of interindividual interactions

elucidated by these experiments does suggest that there should be some threshold population density in the field above which interactions between individuals will mediate increases in locomotion and lead to subsequent mass movement of band members. Obviously, this threshold would be expected to vary by locality due to extrinsic factors such as habitat structure and possibly due to variation in behavioural responses among populations. The precise nature of the stimuli mediating these interindividual interactions, whether they are tactile, visual, auditory or olfactory, was not addressed in this study.

Developmental variation as it relates to the movement of band-forming Mormon crickets is clearly evident in the field. The first few instars typically do not move in bands. Band formation and directional movement tend to take place by the fourth instar and carry on through the adult stage (Cowan 1929; Wakeland 1959; MacVean 1987; Gwynne 2001). Bands continue to move through the reproductive stage, but individuals' movement during this period appears to diminish as they senesce (Lorch & Gwynne 2000; G. A. Sword, P. D. Lorch & D. T. Gwynne, unpublished data). The developmental variation observed here among sixth-instar juveniles, prereproductive and reproductive adults (Table 3, Fig. 2), suggests that movement behaviour may vary even more subtly during ontogeny. However, since these observations were made in the laboratory, their relevance to actual behaviours expressed under field conditions while in a band is indeterminate. It is possible that this variation could be swamped out by behavioural responses to external stimuli while in a group. Although developmental variation in movement behaviour in the immediate presence of stimuli from conspecifics was not explicitly addressed in this study, the data do suggest some slight developmental differences. The expression of all six turning and walking-related behaviours significantly increased in the presence of conspecifics among prereproductive adults, whereas among sixth instars, two turning behaviours, turn angle and meander, failed to change significantly (Table 2, Fig. 2). These findings highlight the need for developmental stage to be controlled as much as possible in future studies of Mormon cricket behaviour in the laboratory as well as in investigations of interindividual interactions and landscape-level movement patterns in the field (e.g. Lorch & Gwynne 2000; G. A. Sword, P. D. Lorch & D. T. Gwynne, unpublished data).

This study is the first to investigate the behavioural mechanisms underlying the movement of migratory band-forming Mormon crickets. It represents one part of an integrated approach to understand how individual behaviours translate into landscape-scale patterns of Mormon cricket band movement. The importance of short-term interindividual interactions in the activation of movement behaviour suggests that Mormon cricket band formation and movement may be best understood if approached as a self-organizing system in which collective movement may be coordinated by relatively simple interactions among group members at high population densities (Camazine et al. 2001; Couzin & Krause 2003). The ability to study the behaviour of individual Mormon crickets in the laboratory, coupled with the fact that the

movement of individuals within mobile bands can be quantified at much larger scales using radiotransmitters (Lorch & Gwynne 2000; G. A. Sword, P. D. Lorch & D. T. Gwynne, unpublished data), will facilitate the use of Mormon crickets as a unique study system for empirical analyses of collective animal movement.

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